TAXONOMY AND PARATAXONOMY OF SOME FOSSIL ANTS (HYMENOPTERA-FORMICIDAE)[1]

By Robert W. Taylor
Biological Laboratories, Harvard University

In current revisionary studies of the ant tribe Ponerini it has become necessary to re-examine the status of various fossils previously placed in the genus *Ponera*. This taxon dates to 1804 and consequently has an unusually complex conceptual and nomenclatural history. The included fossils require special treatment to unravel their part in the resulting snarl.

Thirty-six fossil ants have been placed as *Ponera* or *Ponera*-like by earlier authors but little confidence in the generic assignment of most of them is possible. Some are certainly ponerine, and occasional placement in tribe Ponerini is reasonable. Most species, however, cannot be satisfactorily placed, even to subfamily. The fact is that, to some authors, *Ponera* has served as a "catch-all" for small, possibly ponerine ant fossils, or wing impressions with venation similar to that of *Ponera*.

It is proposed here to review these species and to attempt their allocation into various categories: (1) Formicidae *incertae generis;* (2) Ponerinae *incertae generis;* (3) *Ponera;* (4) (?) *Ponera;* or (5) the form-genus *Poneropsis* Heer, 1867 — as redefined below. The result of sorting the fossil *"Ponera"* in this way has, I believe, some utility relative to evolutionary studies. Species are either placed definitely or reasonably certainly in a known taxon, rendered *"incertae"* at the level at which they *begin* to be uncertain in diagnostic features; or allocated to the phylogenetically meaningless limbo of the parataxon *Poneropsis*. My category "(?) *Ponera*" in general contains species equally well placed in *Ponera* or *Hypoponera*[2], although smaller members of other genera of tribe Ponerini may be included.

---

[1]Based on research supported by the U.S. National Science Foundation, Grant No. GB 1634.

[2]Santschi's subgenus *Ponera* (*Hypoponera*) (1938, Bull. Soc. Ent. France, 43: 8-80) has recently been elevated to full generic status (Taylor, *mss.*). It contains the majority of the living species currently assigned to *Ponera,* and many of its species are superficially *Ponera*-like.

Manuscript received by the Editor May 29, 1964.

The form-genus *Poneropsis* Heer.

In his study of the fossil Hymenoptera of Oeningen and Radoboj, Heer (1867) proposed the use of a formicid form-genus *Poneropsis,* which was defined as follows: ". . . Die fossilen Ameisen welche drei Cubitalzellen in den Oberflügeln und einen einknötigen Hinterleibsstiel, aber keine Einschnürung beim zweiten Hinterleibssegment haben. Sie stimmen im Flügelgeäder und dem einknötigen Stiel mit *Ponera* überein, daher ich sie früher dieser Gattung zugerechnet habe; in der Bildung des Hinterleibes weichen sie aber bedeutend von den *Poneren* ab, namentlich die Arten mit rundem, dickem Hinterleib." Heer's figures show that his "drei Cubitalzellen" are those now referred to as the first and second cubital cells, with the discoidal cell.

Sixteen species were allocated to *Poneropsis* at its inception, including some previously placed in *Ponera* by Heer (1849). No better placement of any of them is possible on the basis of the published data. There appears to be much species-level synonomy among these forms and judging from their size most do not seem close to *Ponera.*

Since the venational type specified for *Poneropsis* is convergently developed in many lines of ant evolution, this "genus" could conceivably contain wing impressions of members of almost every ant subfamily[3]. Moreover the convergent types cannot be separated on the basis of wing venation alone. Accordingly it is pointless to assign such wings indiscriminately to recent taxa to whch they might, at present, be referable. It is far better to assign them definitely to a parataxonomic form-genus which need not be considered in phylogenetic, paleo-zoogeographic, or other studies, rather than to place them randomly in a true taxonomic genus, with presumed affinities to other taxa, extinct or living.

It may be argued that this procedure offers little in comparison with a simple "Formicidae *incertae generis*" allocation. This is partly true, but since Heer's parataxon is available, use of it may as well be maintained, at least until a complete revision of fossil ants is possible. At that time the problem of the use of ant-wing form-genera will

[3]For example, all the following recent genera possess wing venation of the "*Poneropsis*" type: *Gnamptogenys, Eciton, Pseudomyrmex, Messor, Aneuretus, Dolichoderus, Hypoclinea* (See figures of Brown and Nutting, 1950, and Wilson et.al., 1956). Extinct ants with this venation pattern include: *Trachymesopus succinea* (Mayr), *Aphaenogaster mayri* Carp., *Pheidole tertiaria* Carp., *Dolichoderus antiquus* Carp., *Iridomyrmex florissantius* Carp., *Liometopum microcephalus* Carp., and members of the genera *Protazteca* and *Elaeomyrmex* (see Wheeler, 1914 and Carpenter, 1930).

need careful consideration. We must consider the fact that *Poneropsis,* as defined here, contains wings all of which are at approximately the same evolutionary grade of venational reduction (Brown and Nutting, 1950), and that certain genera of ants can be excluded from it, as they never possess such venation. Under such terms we are actually designating fossils more precisely by placing them in *Poneropsis* rather than considering them simply as "Formicidae *incertae generis*". Moreover, and this is an important consideration, use of this parataxon allows convenient placement of such fossils in a single group easily referred to by those seeking examples of such venational types for other studies.

I propose the following redefinition of *Poneropsis.* The nomenclature used for wing veins is that of Brown and Nutting (1950).

Form-genus, *Poneropsis* Heer, 1867

Hymenopterous forewings, apparently belonging to family Formicidae, and either alone or attached to fossils otherwise unclassifiable, and of a type not known to be associated with remains yielding more satisfactory placement.

Two closed, fully separated, cubital cells (the 1st and 2nd) present. First discoidal cell always closed; second discoidal open or closed. Radial cell open or closed. The adventitious longitudinal vein Rsx, and the first radial cross vein (1r), or a stub of it, absent.[4] Second radial cross vein (2r) usually arising near the anterior base of the radio-medial cross vein (r-m), and always reaching the stigma at a point distal to the first quarter of its posterior border.[5] The second free abscissa of the median vein may be contracted, so that the posterior end of Rs + M2 lies adjacent to the anterior end of the (first) medio-cubital cross vein (m-cu); or fusion of elements in this area may cause the base of the former vein to lie distal to that of the latter. First abscissa of median vein (Mf1) lying proximal, distal, or adjacent to the anterior base of the cubital anal cross vein (cu-a) where it meets CuA.[6]

Specimens with a two-segmented petiole and *Poneropsis*-type wing

[4]Wings referable to primitive ponerines and myrmeciines such as *Platythyrea, Myrmecia,* and some Amblyoponini are, therefore, excluded, (Brown and Nutting, 1950; Brown, 1960).

[5]This clause allows distinction of *Eoponera* Carpenter (1929) — see Brown and Nutting, fig. 6.

[6]As Brown and Nutting point out, it is possible that origin of Mf1 well proximal of cu-a is a key character identifying doryline ants. If this should prove to be so, the above diagnosis could be easily modified to preclude wings of fossil Dorylinae.

venation must be placed in the Myrmicinae or one of the other applicable subfamilies. If the node is one-segmented and other characters of the gaster (presence of sting, etc.) are visible, then placement to subfamily should be possible.

The many qualifications made to the simple basic diagnosis, "two closed cubital cells, and a single closed discoidal," allow inclusion in *Poneropsis* of virtually all known ants with these primary characters. I do not wish to imply that study of wing vein patterns, such as was pioneered by Brown and Nutting, should not be applied to ant fossils. These authors have shown, however, that extreme parallelism may take place in the details of venational reduction in the various ant subfamilies, with the result that amazingly similar wings may be produced in divergent lines. The various ranges specified in my diagnosis simply cover all stages in venational reduction known to show such parallelism in wings with two cubital cells and at least one closed discoidal cell.

With the possible exception of the feature discussed in footnote 6 of the diagnosis, no alternative condition in these venational characters, or combination of conditions, is currently known to diagnose unequivocally any ant taxon.

Ponera and Poneropsis species described by Heer (1849, 1867).

In 1849, Heer described nine extinct species in *Ponera* from the Miocene of Radoboj, Oeningen and Parschlung, Croatia. In his 1867 paper four of these were referred to the newly defined formgenus *Poneropsis,* and thirteen further specific or infraspecific forms were also described, all in *Poneropsis.*

I have been unable to justify any of the generic assignments in *Ponera,* and find that most of Heer's species, both of *Ponera* and *Poneropsis,* can be assigned to *Poneropsis* as defined above, thus conveniently disposing of them. Others, including some placed by Heer in *Poneropsis,* do not appear referable there on the basis of his figures, since the wing venation is too incompletely shown in the fossils or the wings appear to have had only a single cubital cell.

The history and present status of Heer's (1849) *Ponera* species is summarized in the following Table. The two species considered here to be "Formicidae *incertae generis*" were based on remains too incomplete to allow better allocation.

Mayr (1867) and Popov (1932) have both referred to some of these species, assigning them with or without query to *Ponera.* Repetition of Mayr's names serves no purpose; most of them were originally placed in *Poneropsis* (by Heer) and so Mayr's combinations do not constitute nomenclatural occupation in *Ponera,* since none of

Species placed in *Ponera* by Heer 1849	Species placed in *Ponеropsis* by Heer 1867	Current assignment
affinis	*affinis*	Formicidae *incertae generis*
crassinervis	—	*Poneropsis*
croatica	—	*Poneropsis*
elongatula	*elongatula*	Formicidae *incertae generis*
fuliginosa (with subspecies *oeningensis* and *radoboj*)	*fuliginosa*	*Poneropsis*
globosa	—	*Poneropsis*
longaeva	—	*Poneropsis*
nitida	*nitida*	*Poneropsis*
ventrosa	—	*Poneropsis*

them are now considered to belong in the genus. Popov's citations are important, however, as he used some of the names originally assigned to *Ponera* by Heer, thus firmly establishing them in modern systematic nomenclature. Those involved are *croatica, crassinervis* (incorrectly spelled as *crassicornis*), *ventrosa, longaeva* and *globosa.*

All of the additional thirteen species described in *Poneropsis* in 1867 appear to be satisfactorily placed, except *elongata, anthracina, imhoff,* and *stygia* in which the wings are too incompletely preserved to allow allocation — they should be considered "Formicidae *incertae generis*".

A further species, *Ponera veneraria,* was described by Heer in his *Urwelt der Schweiz* (1865). This species was later transferred to *Poneropsis* in the 1879, second edition of the same work. On the basis of Heer's 1865 figure I concur with Handlirsch (1908) that this species is best placed as Formicidae *incertae generis.* The name was misspelled "*vernaria*" by Handlirsch.

Fossil *Ponera* described by authors other than Heer.

The following list, as far as I am aware, includes all ant fossils allocated to *Ponera* by authors other than Heer. This includes those which have since been placed elsewhere by previous authors, whose reassignments are discussed below with my own opinions on the proper placement of all the species listed here. The appropriate references may be obtained in the bibliography.

1. *Ponera atavia* Mayr, 1868: 72, figs. 66-69, female, male. Oligocene — Baltic Amber. Wheeler, 1914: 38, fig. 9. worker.
2. *Ponera brodiei,* Giebel, 1856: 173. This forewing fragment, originally described as an ant, *Formicium brodiei,* by Westwood (1854) has been subsequently placed in the Jurassic siricoid family Anaxyelidae (Maa, 1949).
3. *Ponera gracilicornis* Mayr, 1868: 72, worker, Baltic Amber.
4. *Ponera hendersoni* Cockerell, 1906, female. Miocene-Florissant.
5. *Ponera hypolitha* Cockerell, 1915: 483, plate 64, figs. 3-4, wing impression. Oligocene — Gurnet Bay, Isle of Wight.
6. *Ponera*(?) *leptocephala* Emery, 1891: 8, plate 1, figs. 3, 4, female. Miocene — Sicilian Amber.
7. *Ponera minuta* Donisthorpe, 1920: 85, plate 5, fig. 4, male (?). Oligocene, Gurnet Bay, Isle of Wight.
8. *Ponera rhenana* Meunier, 1917, wing impression. Oligocene — Bavaria.
9. *Ponera scitula* Clark, 1934, listed from Tertiary, Allendale, Australia by Oke (1957).
10. *Ponera succinea* Mayr, 1868: 72, female. Oligocene — Baltic Amber.
11. *Ponera*(?) *umbra* Popov, 1933: 17, fig. 1, female. Miocene — Kuban Caucasas.

Of these species only one, *P. atavia* Mayr, is considered here to be satisfactorily referred to *Ponera. P. succinea* Mayr was transferred to *Euponera (Trachymesopus)* — now *Trachymesopus* — by Wheeler (1914), on grounds which are entirely acceptable. *P. gracilicornis* Mayr is too large to be considered a *Ponera* (Wheeler, 1914), but Mayr's assignment of the species to the Ponerinae is probably dependable — the species is considered here as "Ponerinae *incertae generis*". (?)*P. leptocephala* Emery is best assigned with reservation to *Ponera.* This form is evidently close to *Ponera* or *Hypoponera,* but has very long legs and antennae, and the eyes appear to be placed exceptionally far back on the head. It may belong to a distinct genus as yet undiagnosed, but it would be premature to so assign it on the basis of Emery's description and figures. *P.*(?) *umbra* Popov also seems best assigned to (?) *Ponera.* It appears close to *Ponera* although it could equally well be a *Hypoponera* or a member of some other small genus of the tribe Ponerini.

I propose the following NEW COMBINATIONS in *Poneropsis: Poneropsis hypolitha* (Cockerell), and *Poneropsis rhenana* (Meunier), these are both wing impressions and cannot be assigned more satisfactorily at present. *P. minuta* is considered "Formicidae *incertae*

generis"; no reason whatsoever was presented by Donisthorpe to justify its placement in *Ponera,* and no satisfactory diagnostic characters are given in his figure or description. *P. hendersoni* Cockerell has been shown by Carpenter (1930) to be referable to the extinct genus *Protazteca.* The recent Australian species, *Hypoponera scitula* (Clark) (NEW COMBINATION from *Ponera),* was listed as a tertiary fossil from Allendale, Victoria, under the name *Ponera scitula,* by Oke (1957). I have not seen the specimens involved, but since they were determined by Clark, the assignment is presumably trustworthy.

Fossil names and their nomenclatural status.

According to the principle of homonomy certain of the specific names given above are no longer available for use in *Ponera.* The eleven names assigned by Heer in 1849 (see list, p. 138), and the ten species, excluding *brodei,* assigned by subsequent authors and listed above on page 139 are in this category, as is the specific name *veneraria* Heer (1865).

Literature Cited

Brown, W. L., Jr.

1960. Contributions toward a reclassification of the Formicidae. III tribe Amblyoponini. Bull. Mus. Comp. Zool. Harv., 122 (4): 145-230.

Brown, W. L., Jr., and W. L. Nutting

1950. Wing venation and the phylogeny of the Formicidae. Trans. Amer. Ent. Soc., 75: 113-132.

Carpenter, F. M.

1929. A fossil ant from the lower Eocene (Wilcox) of Tennessee. J. Wash. Acad. Sci., 19: 300-301.

1930. The fossil ants of North America. Bull. Mus. Comp. Zool. Harv., 70 (1): 1-66, 11 pls.

Cockerell, T. D. A.

1906. A new fossil ant. Ent. News, Philad., 17: 27-28.

1915. British fossil insects. Proc. U.S. Nat. Mus., 49: 469-499, 6 pls.

Donisthorpe, H. St. J. K.

1920. British Oligocene ants. Ann. Mag. Nat. Hist., 6: 81-94, 1 pl.

Emery, C.

1891. Le formiche dell' ambra Siciliana nel museo mineralogico dell' universitadi Bologna. Mem. R. Acc. Bologna, 5 (1): 141-165, 3 pls.

Giebel, C. G.

1856. *Insecten und Spinnen der Vorwelt.*, Brodhaus, Leipzig., pp. 1-511.

Handlirsch, O.

1908. *Die Fossilen Insekten.* W. Engelmann, Leipzig., pp. 1-1430.

Heer, O.
1849. Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien. II. Neue Denkschr. Allgem. Schweiz. Geol. Ges. Naturw., 11: 1-264, 17 pls., (pp. 145-153).
1867. Fossile Hymenoptera aus Oeningen und Radoboj. *Ibid.,* 22 (4): 1-42, 17 pls.
Maa, T.
1949. A synopsis of Asiatic Siricoidea with notes on certain exotic and fossil forms. Notes d'Ent. Chinoise, Shanghai, 13 (2): 11-189.
Mayr, G. L.
1867. Vorläufige Studien über die Radoboj-formiciden. Jahrb. Geol. RchsAnst. Wien., 17: 47-62, 1 pl.
1868. Die Ameisen des baltischen Bernsteins. Beitr. Naturk. Preuss., 1: 1-102, 5 pls.
Meunier, F.
1917. Sur quelques insectes des lignites de l'Aquitanien de Rott sept Montagnes (Preusse rhénane). Verh. Akad. Wet. Amst., (2) 20 (1): 1-17.
Oke, C.
1957. Fossil Insecta from Cainozoic Resin at Allendale, Victoria. Proc. R. Soc. Victoria. n. s., 69: 29-31.
Popov, V.
1932. Two new fossil ants from Caucasus (Hymenoptera-Formicidae). Trav. Inst. Paléozool. Acad. Sci. U.S.S.R., 2: 17-21.
Taylor, R. W.
mss. A monographic revision of the ant genus *Ponera* (Hymenoptera-Formicidae). To appear in Bull. Mus. Comp. Zool. Harv.
Westwood, J. O.
1854. Contributions to fossil entomology. Quart. J. Geol. Soc. Lond., 10: 378-396.
Wheeler, W. M.
1914. The ants of the Baltic Amber. Schrift. Physick. Oken. Gesell. Königsberg, 55: 1-142, 66 figs.
Wilson, E. O., and T. Eisner, G. C. Wheeler, J. Wheeler
1956. *Aneuretus simoni* Emery, a major link in ant evolution. Bull. Mus. Comp. Zool. Harv., 115: 81-99, 3 pls.